

# Temperature response of ex-situ greenhouse gas emissions from tropical peatlands: Interactions between forest type and peat moisture conditions

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## ARTICLE INFO

Handling Editor: Jan Willem Van Groenigen

### Keywords:

Climate change

Carbon dioxide

Methane

Peatland

Moisture status

Temperature response

Tropical

## ABSTRACT

Climate warming is likely to increase carbon dioxide (CO<sub>2</sub>) and methane (CH<sub>4</sub>) emissions from tropical wetlands by stimulating microbial activity, but the magnitude of temperature response of these CO<sub>2</sub> and CH<sub>4</sub> emissions, as well as variation in temperature response among forest types, is poorly understood. This limits the accuracy of predictions of future ecosystem feedbacks on the climate system, which is a serious knowledge gap as these tropical wetland ecosystems represent a very large source of greenhouse gas emissions (e.g. two-thirds of CH<sub>4</sub> emissions from natural wetlands are estimated to be from tropical systems). In this study, we experimentally manipulated temperatures and moisture conditions in peat collected from different forest types in lowland neotropical peatlands in Panama and measured how this impacted ex-situ CO<sub>2</sub> and CH<sub>4</sub> emissions. The greatest temperature response was found for anaerobic CH<sub>4</sub> production ( $Q_{10} = 6.8$ ), and CH<sub>4</sub> consumption (mesic conditions,  $Q_{10} = 2.7$ ), while CO<sub>2</sub> production showed a weaker temperature response ( $Q_{10} < 2$ ) across the three moisture treatments. The greatest temperature response of CO<sub>2</sub> production was found under flooded oxic conditions. Net emissions of CO<sub>2</sub> and CH<sub>4</sub> were greatest from palm forest under all moisture treatments. Furthermore, the temperature response of CH<sub>4</sub> emissions differed among dominant vegetation types with the strongest response at palm forest sites where fluxes increased from  $42 \pm 25$  to  $2166 \pm 842$  ng CH<sub>4</sub> g<sup>-1</sup> h<sup>-1</sup> as temperatures were raised from 20 to 35 °C. We conclude that CH<sub>4</sub> fluxes are likely to be more strongly impacted by higher temperatures than CO<sub>2</sub> fluxes but that responses may differ substantially among forest types. Such differences in temperature response among forest types (e.g. palm vs evergreen broad leaved forest types) need to be considered when predicting ecosystem greenhouse gas responses under future climate change scenarios.

## 1. Introduction

Global atmospheric methane (CH<sub>4</sub>) and carbon dioxide (CO<sub>2</sub>) concentrations are increasing as a consequence of human activities such as fossil fuel burning and land use change (IPCC, 2013). The resulting climatic changes may further increase greenhouse gas (GHG) emissions from terrestrial biomes, creating a positive feedback loop resulting in additional climate warming; however, such feedbacks will differ among ecosystems. Wetlands are important components of the global carbon cycle and exchange large quantities of CH<sub>4</sub> and CO<sub>2</sub>; indeed, they are recognised as the largest individual natural source of atmospheric CH<sub>4</sub>, a potent GHG (e.g. Lelieveld, 1998; Bridgman et al., 2013; IPCC, 2013).

Two thirds of wetland CH<sub>4</sub> emissions are estimated to originate from natural tropical ecosystems in Southeast Asia, Africa and the Neotropics (Melton et al., 2013). These wetlands are also large emitters of CO<sub>2</sub>,

estimated at  $4540 \pm 1480$  Tg CO<sub>2</sub> year<sup>-1</sup> (Sjögersten et al., 2014). Furthermore, tropical peatlands acts as globally important stores of carbon (C) (Page et al., 2011). The CO<sub>2</sub> and CH<sub>4</sub> emissions of tropical peatlands are regulated by water table/redox state (Jauhiainen et al., 2005; Hoyos-Santillán, 2014), quantity and quality of litter inputs (Wright et al., 2011; Sjögersten et al., 2014; Hoyos-Santillán et al., 2015) and temperature (Hirano et al., 2009). However, despite the significance of tropical wetlands in the global carbon cycle, the temperature response of GHG emissions from tropical peatlands is largely unknown (see Hirano et al., 2009), limiting our ability to predict climate change responses of their CO<sub>2</sub> and CH<sub>4</sub> emissions despite their high emissive potential (Bridgman et al., 2013).

This is a critical knowledge gap as we do not know if the wealth of data exploring temperature responses of CH<sub>4</sub> and CO<sub>2</sub> fluxes from higher latitude ecosystems can be transferred to tropical systems. It is

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for example plausible that tropical wetland microbial communities are adapted to higher temperatures, rendering them less sensitive to elevated temperatures than those in higher latitudes. Alternatively, differences in soil organic matter chemistry between high and low latitude wetlands may result in substantial differences in the temperature response of decomposition and release of GHGs (Lloyd and Taylor, 1994; Bosatta and Ågren, 1999; Fierer et al., 2005).

Tropical peatlands are under threat from climate change, which could substantially affect their water balance, and resultant CO<sub>2</sub> and CH<sub>4</sub> emissions (Furukawa et al., 2005; Li et al., 2007; Hooijer et al., 2010; Laiho, 2006; IPCC, 2013). With regards to climate change, current predictions indicate air temperatures in the neotropics and Southeast Asia will be 3–4 °C higher by 2100 and 5–7 °C higher by 2200 (IPCC, 2013). To date precipitation changes in the Amazon region have been associated with wetter wet seasons and drier dry season but there are no strong overall trends for the region (Almeida et al., 2017). In the future precipitation in the neotropics is predicted to decrease by ca. 10% by 2100 (ca. 350 mm less per year) and by 20–40% by 2200 (up to 1400 mm less per year) under the Intergovernmental Panel on Climate Change (IPCC) scenario RCP 8.5 (IPCC, 2013) although, model predictions of changes in precipitation patterns are more uncertain than the temperature predictions and patterns varies between inland and coastal areas (Chao et al., 2008; Oueslati et al., 2016). Together these changes are predicted to result in drier soils (IPCC, 2013). Increased temperature can be expected to increase microbial decomposition rates directly (Hirano et al., 2009), while lower water tables could result in large increases in soil CO<sub>2</sub> losses to the atmosphere and reduced CH<sub>4</sub> emissions (Jauhiainen et al., 2005; Couwenberg et al., 2010).

The “carbon-quality temperature hypothesis” postulates that the temperature sensitivity of decomposition processes increases with the complexity (recalcitrance) of soil organic matter, because larger activation energies are required for its catabolism under aerobic conditions (Lloyd and Taylor, 1994; Bosatta and Ågren, 1999; Fierer et al., 2005). In the context of tropical peatlands, this would suggest that climate change could result in decomposition of recalcitrant organic matter as temperatures increase. Furthermore, it is plausible that the dominance of palms and evergreen broad leaved trees in tropical peatlands result in substantially different soil organic matter chemistry (Hoyos-Santillán et al., 2015) compared to higher latitude wetlands where peat formation is often driven by graminoid and moss litter inputs (Turetsky et al., 2014) which is likely to affect the temperature response of peat decomposition. For example, recalcitrant lignin and long chain fatty acids from wood and evergreen leaf litter inputs, respectively, represent a large component of litter inputs in tropical peatlands (Sjögersten et al., 2014). According to the carbon-quality temperature hypothesis this would suggest that soil organic matter in tropical peatland may be more responsive to elevated temperature than higher latitude ecosystems.

Water logging and anaerobic conditions have been shown to affect the temperature response of C mineralisation strongly: CH<sub>4</sub> production in both subtropical and high latitude wetlands appears to be more sensitive to temperature than either aerobic or anaerobic CO<sub>2</sub> production (Dunfield et al., 1993; van Hulzen et al., 1999; Inglett et al., 2012; Treat et al., 2014). When comparing the relative impact of temperature on CH<sub>4</sub> production and oxidation, CH<sub>4</sub> oxidation does not appear to increase with temperature as rapidly as CH<sub>4</sub> production (Dunfield et al., 1993; Inglett et al., 2012), so higher temperatures may increase net CH<sub>4</sub> emissions. It is important to consider temperature response in the context of moisture status as soils are predicted to come drier in the tropics in response to climate change as there are strong links between moisture conditions/water tables position and GHG emissions (Jauhiainen et al., 2005; Couwenberg et al., 2010).

The aim of this study is therefore to investigate how increasing peat temperatures and changes in moisture levels of neotropical peatlands may interact to control ex situ CO<sub>2</sub> and CH<sub>4</sub> emissions. To achieve this we ran controlled experiments with peat from lowland neotropical peatlands to determine the temperature responses for ex situ CO<sub>2</sub> and

CH<sub>4</sub> fluxes under both aerobic and anaerobic conditions. The experiment consisted of incubating peat at a range of temperatures and moisture states. As these peatlands are heterogeneous with regards to vegetation and soil nutrient status (Troxler, 2007; Sjögersten et al., 2011) we investigated the impact of moisture and temperature treatments on CO<sub>2</sub> and CH<sub>4</sub> emissions from peat samples extracted from four forest types commonly found in peatlands in the neotropics (Phillips et al., 1997; Nahlik and Mitsch, 2011; Roucoux et al., 2013): palm, mixed, hardwood and stunted forest.

## 2. Methods

### 2.1. Study area

The San San Pond Sak wetland complex is a 164 km<sup>2</sup> mosaic of freshwater and marine-influenced wetlands in Bocas del Toro Province on the Caribbean coast of western Panama (Cohen and Stack, 1996). Recognised internationally as a largely pristine wetland of special scientific interest (Ramsar site #611), San San Pond Sak includes the significant 80 km<sup>2</sup> Changuinola peat deposit, an ombrotrophic domed peatland to the south east of Changuinola river (Phillips et al., 1997). The oldest deposits in the Changuinola peatland are estimated to have been formed 4000–4500 years ago and are > 8 m deep in the central areas (Phillips et al., 1997). Peat at the edges of the peatland is younger and ca. 2 m deep.

Seven distinct phasic plant communities cover the peatland (Phillips et al., 1997). Starting from the periphery, these communities have been designated as (i) *Rhizophora mangle* mangrove swamp, (ii) mixed back mangrove swamp, (iii) *Raphia taedigera* palm forest swamp, (iv) mixed forest swamp (consisting of both palm and evergreen broadleaved hardwood trees), (v) *Camposperma panamensis* forest swamp, (vi) sawgrass/stunted forest swamp and (vii) *Myrica-Cyrilla* bog-plain. In this study we focused on (iii) to (vi) of these phasic communities as these represent the dominant forest types in the peatland. For simplicity we denote these as palm forest, mixed forest, hardwood forest, and stunted forest throughout the paper. The forest is mainly unaffected by human activities although occasional small scale selective logging is evident in areas close to the coast and rivers. Nutrient levels in the peat and plant tissue vary greatly among vegetation communities and are generally low in the interior and higher towards the edge of the peatland (Troxler, 2007; Sjögersten et al., 2011). The low nutrient content in the interior is reflected by reduced microbial activity, with higher microbial biomass C:N and C:P ratios and up-regulation of the activity of extracellular enzymes involved in nutrient acquisition (Sjögersten et al., 2011; Cheesman et al., 2012). Furthermore, in situ (i.e. measurement in the field) CO<sub>2</sub> and CH<sub>4</sub> fluxes along this vegetation transect did not appear to reflect peat nutrient availability (Wright et al., 2013), while laboratory incubations (ex situ) of drained surface peat samples show lower CO<sub>2</sub> production in substrates from the interior than sites closer to the edge of the peatland (Sjögersten et al., 2011).

A weather station in the nearby town of Bocas del Toro, Isla Colon, ca. 10 km from the peatland, shows the area has a mean annual temperature of 25.9 °C with low intra-annual variability, and recorded a mean annual precipitation of 3092 mm between 2003 and 2011 (Hoyos-Santillán et al., 2015). Rainfall is continuous throughout the year with no pronounced dry season, although there are two distinct periods of lower rainfall (February–March and September–October). Water tables in these peatlands are dynamic and mainly fluctuate around ± 0.2 m from the surface, with water tables increasing rapidly after intense rainfall events and dropping to or below the surface in between rainfall events (Wright et al., 2013; S. Sjögersten, pers. obs.). During occasional, prolonged dry (i.e. no rainfall) periods, the water table can drop as low as –40 cm (Hoyos-Santillán, 2014). Conversely, high rainfall events can cause the water tables to rise above the peat surface (normally no more than ca. 10–20 cm). Mean peat temperature 10 cm below the surface is ca. 25 °C and shows little intra-annual

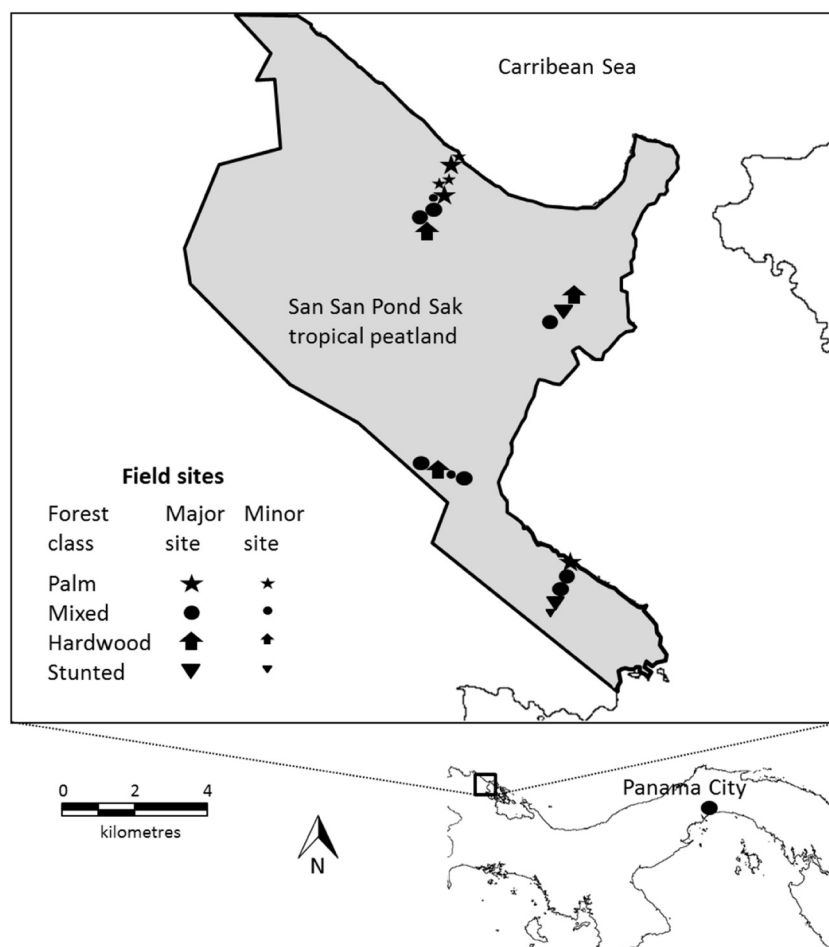


Fig. 1. Map of the San San Pond Sak peatland showing the sampling sites used in the field campaign.

variation (Wright et al., 2013).

## 2.2. Field sampling strategy

For the sampling campaign we established four transects (ca. 1 km) (Fig. 1). Transects were selected following assessment of satellite imagery of the study area; in each case there was evidence of vegetation transition from the coast or river inlets towards the interior of the peatland. Along these transects we collected peat samples for the incubation study from palm forest ( $n = 6$  sites), mixed forest ( $n = 9$ ), hardwood forest ( $n = 3$ ) and stunted forest ( $n = 3$ ), i.e. 21 sites in total. More detailed description of these four forest types are in Sjögersten et al. (2011). Note that not all forest types occurred along all transects. At a subset of sites denoted “major sites” (Fig. 1), we carried out a more detailed site characterisation including in situ  $\text{CO}_2$  and  $\text{CH}_4$  surface exchange measurements to serve as background data for the incubation study.

## 2.3. Collection and analysis of field gas samples

At the major sites we established  $5 \times 5$  m plots using a set of random coordinates. Within each plot we made a visual assessment of the proportion of the area covered by standing water (done independently by two people). The depth of pools of standing water relative to the peat surface was determined in three random locations within the plot. Air and peat temperature (at 10 cm depth) was measured.

As part of the site characterisation the in situ net exchange surface fluxes of  $\text{CO}_2$  and  $\text{CH}_4$  were determined at the major sites; however, as

gas sampling was carried out at only one time point, these data only give a snapshot of in situ fluxes and should be interpreted carefully. Gas samples were collected from the four corners of the  $5 \times 5$  m plots using the closed static chamber technique (Denmead, 2008). Gas sampling was made between 10 a.m. and 4 p.m. concurrently with other plot characterisation measurements. The chamber volume was  $9 \text{ dm}^3$  and the exchange surface  $0.07 \text{ m}^2$ . To avoid root and soil disturbance the chambers was sealed to the water logged peat surface by gently placing them into the peat or floating them on the water surface when the sampling location was flooded. Air samples were collected through a Suba-Seal® valve (Sigma-Aldrich, St-Louis, USA) using a hypodermic needle and 20 mL a syringe. Samples of 20 mL were collected after 1, 3, 5 and 7 min and injected into evacuated 12 mL Exetainer serum vials (Labco, Ceredigion, UK) giving a slight over-pressure in the vial to allow for leak detection. Samples were collected by a team member reaching over the sampling chamber from ca 1 m distance. There was no movement around the chamber during the sampling period.

All gas samples were analysed by gas chromatography (GC 2014, Shimadzu, Milton Keynes, UK) using a 1 mL sampling loop and a molecular sieve column (12 m, 0.53 mm internal diameter);  $\text{CO}_2$  concentration was determined by thermal conductivity and  $\text{CH}_4$  by flame ionisation. Fluxes of  $\text{CO}_2$  and  $\text{CH}_4$  were calculated using the ideal gas law for sampling points which met the assumption of linear (or near linear) gas accumulation during the closure period (Wright et al., 2013).

At all plots a peat sample from 0 to 10 cm depth, ca.  $5 \times 5 \times 5$  cm volume, was collected for incubation experiments and chemical characterisation. Peat depth was measured by pushing 2 cm diameter connecting rods through the peat (low density  $0.1 \text{ g cm}^{-3}$ ) as far as the

underlying marine sediments (clay or sand; higher density  $> 1 \text{ g cm}^{-3}$ ). The accuracy of this method was tested by comparison with depths determined using a Russian peat borer for a subset of sites; this indicated that the rods were accurate, although depths might be overestimated in areas where a transition occurs from peat to soft organic rich marine clay sediments (error estimated at 0–100 cm based on peat core data (Hoyos-Santillán, 2014; Sjögersten et al., unpublished data)).

#### 2.4. Peat chemical characterisation

The collected peat samples were analysed for total elements and extractable nutrients. Peat samples were transported to the laboratory (approx. 4 h), stored at  $-20^\circ\text{C}$  and shipped frozen to the UK to avoid depletion of labile substrates during storage. We acknowledge that the freezing may have impacted on activity of the microbial community; however, comparisons of microbial enzyme activities in tropical forest soils do not suggest that freezing has a negative impact on the activities of enzymes involved in microbial C acquisition, compared to storage at room temperature (Turner and Romero, 2010). Prior to analysis, peats were thawed at  $4^\circ\text{C}$ . After thawing, roots were removed by hand with tweezers prior to analysis but fine roots inevitably remained in some samples. Moisture content was determined by drying subsamples of peat at  $105^\circ\text{C}$  for 24 h. Peat pH and conductivity were determined using a glass electrode and a portable conductivity meter (Hanna Instruments), respectively, in a 1:2 ratio of fresh peat to deionized water.

Dissolved organic C and nitrogen (N) fractions were extracted by shaking 40 g of fresh soil in 75 mL of  $0.5 \text{ M K}_2\text{SO}_4$  for 1 h. Extracts were centrifuged (8000g, 15 min) and dissolved C and N were determined after a five-fold dilution by automated combustion and gas chromatography on a TOC-VCSH analyzer (Shimadzu UK Ltd., Milton Keynes, UK), coupled with a total N measuring unit (TNM-1, Shimadzu UK Ltd., Milton Keynes, UK). The fulvic:humic acid ratio and the related degree of humification in dissolved organic matter were estimated by spectrophotometric analysis (Grayson and Holden, 2012). Porewater samples were passed through cellulose filters (Whatman Grade 1,  $11 \mu\text{m}$ ) and absorbance was measured at 465 and 665 nm (U-2010, Hitachi UV-VIS Spectrophotometer). The absorbance values were then used to estimate the  $E_{465}/E_{665}$  index (Uyguner and Bekbolet, 2005) where a greater ratio indicates more labile constituents. Ammonium in the  $\text{K}_2\text{SO}_4$  (see above) extracts was determined by colorimetry at 635 nm following reaction with phenol and hypochlorite. Readily-exchangeable phosphate was determined by extraction with anion exchange membranes (AEM) using a method based on that described by Myers et al. (2005). Peat (20 g fresh weight) was shaken for 24 h with 80 mL deionized water and five anion-exchange resin strips ( $1 \times 4 \text{ cm}$ ; manufactured by BDH Prolabo and distributed by VWR International, Lutterworth, Leicestershire, UK). The strips were rinsed in deionized water and the phosphate recovered by shaking for 1 h in 50 mL of  $0.25 \text{ M H}_2\text{SO}_4$ . Multi-element analysis of diluted solutions was undertaken by ICP-MS (Thermo-Fisher Scientific iCAP-Q; Thermo Fisher Scientific, Bremen, Germany). The instrument was run using standard mode (STD) in which the collision cell is evacuated. Samples were introduced from an autosampler (Cetac ASX-520) incorporating an ASXpress™ rapid uptake module through a PEEK nebulizer (Burgener Mira Mist). Internal standards were introduced to the sample stream on a separate line via the ASXpress unit and included Ge ( $10 \mu\text{g L}^{-1}$ ), Rh ( $10 \mu\text{g L}^{-1}$ ) and Ir ( $5 \mu\text{g L}^{-1}$ ) in 2% trace analysis grade (Fisher Scientific, UK)  $\text{HNO}_3$ . External multi-element calibration standards (Claritas-PPT grade CLMS-2 from SPEX Certiprep Inc., Metuchen, NJ, USA) included Ag, Al, As, Ba, Be, Cd, Ca, Co, Cr, Cs, Cu, Fe, K, Li, Mg, Mn, Mo, Na, Ni, P, Pb, Rb, S, Se, Sr, Tl, U, V and Zn, in the range  $0\text{--}100 \mu\text{g L}^{-1}$  (0, 20, 40,  $100 \mu\text{g L}^{-1}$ ). Phosphorus also utilized in-house standard solutions ( $\text{KH}_2\text{PO}_4$ ). In-sample switching was used to measure P in STD mode. Sample processing was undertaken using Qtegra™ software (Thermo-Fisher Scientific) utilizing external cross-calibration between pulse-counting and analogue detector modes when required. Loss on ignition

(LOI) was determined as mass loss following ignition for 7 h at  $550^\circ\text{C}$  (Heiri et al., 2001).

#### 2.5. Incubation procedures

The collected peat samples were also measured for ex situ GHG fluxes under three moisture treatments: flooded anaerobic, flooded oxic, and mesic conditions. The anaerobic treatment models long-term raised water tables. The flooded oxic treatment models oxygenated high water table conditions (e.g. following rainfall). The mesic treatment reflects low surface moisture during periods of low rainfall when water tables drop. Each of this treatment was placed to four different temperatures: 20, 25, 30 and  $35^\circ\text{C}$  (reflecting the in situ annual air temperature range incremented by  $5^\circ\text{C}$  to reflect climate warming predictions IPCC (2013)). The assumption made here are that peat temperatures will increase to the same extent as air temperatures.

For the incubation, 100 mL serum bottles were filled with 5 g of field moist peat from each peat sample collected from the peat surface (0–10 cm). For the anaerobic treatment 10 mL of deionized water was added to the peat and the peat water mixture was bubbled with  $\text{N}_2$  vigorously to create oxygen-free conditions and to fill the head space with  $\text{N}_2$  (Hoyos-Santillán et al., 2016). The bottles were then capped using black butyl stoppers and crimped, and the bottles were placed in four different incubators set at the required temperature. The peat mesocosms were then left in the incubator for three weeks to allow the microbial communities to acclimatise, after this time a 5 mL gas sample was taken from the bottle and analysed for  $\text{CO}_2$  and  $\text{CH}_4$  using a GC (see above) to assess anaerobic gas production. This sampling was repeated after one week.

For the flooded oxygenated treatment the head space was aerated and then shaken for ca 1 min to encourage  $\text{O}_2$  mixing. This procedure was repeated daily for a week to stimulate aerobic heterotrophic activity while the bottles were kept in their respective incubators (modified from Hoyos-Santillán et al. (2016)). At the end of the week, aerobic  $\text{CO}_2$  and  $\text{CH}_4$  production rates were assessed. This was done by first bubbling air with known  $\text{CO}_2$  and  $\text{CH}_4$  concentrations ( $127 \pm 1.9$  and  $1.5 \pm 0.1 \text{ ppm}$ , for  $\text{CO}_2$  and  $\text{CH}_4$ , respectively) through the peat for 1 min. After flushing, the headspace bottles were capped using butyl stoppers. The bottles were immediately returned to their incubators for ca. 1 h (Dunfield et al., 1993; Inglett et al., 2012) after which a 5 mL gas sample was taken from each bottle for determination of  $\text{CH}_4$  and  $\text{CO}_2$ . Gas fluxes were calculated using the concentration difference between the initial head space concentrations compared to those after one hour incubation.

The mesic moisture treatment involved incubation of the bottles at  $30^\circ\text{C}$  to allow moisture to evaporate from the bottles, reflecting natural evaporation conditions during low rainfall periods. The evaporation rate differed among samples and, rather than letting the peat dry for a set time, we regularly checked the peat moisture status visually, and conditions were considered mesic when there was no “free” water visible in the bottles’ peat but the peat was still moist. The gravimetric moisture content used for the mesic incubations ranged between 300 and 800% (dry weight basis), reflecting the high and variable water absorption capacity of the peat. After mesic conditions were achieved, the bottles were covered in parafilm and placed back in their respective temperature incubators for two weeks to equilibrate.  $\text{CO}_2$  and  $\text{CH}_4$  production rates were assessed by bubbling air with known  $\text{CO}_2$  and  $\text{CH}_4$  concentrations following the same procedure as described in the section above.

#### 2.6. Data analysis

At the end of the temperature incubations  $Q_{10}$  values was calculated in the instances when exponential growth models fitted the GHG flux data (Lloyd and Taylor, 1994). The  $Q_{10}$  value describes the increase in respiration rates with a  $10^\circ\text{C}$  increase in temperature and was



calculated using Eq. (1) with  $k$  being the rate constant

$$Q_{10} = e^{10k}. \quad (1)$$

Analyses of variance on the impact of the treatments on GHG fluxes were performed using the Residual Maximum Likelihood method (REML). We ran mixed linear models to tease apart the impact of forest type, temperature and moisture regime on the  $\text{CO}_2$  and  $\text{CH}_4$  fluxes. In the model forest type, temperature and moisture treatment were used as fixed effects, and transect and site as random effects. The  $\text{CH}_4$  fluxes were log-transformed prior to analysis. Differences in site properties were analysed using REML with forest type as fixed effect and site as random effect.

We investigated the relationship between temperature and gas fluxes using regression analysis. Where required, the flux data were log-transformed to meet normality assumptions. Normal distributions, homogeneity and homoscedasticity of residuals were checked using QQ-plots and scatter-plots for all statistical models. Statistical analyses were performed in GenStat (VSN International, 2011).

### 3. Results

#### 3.1. Site and chemical properties

All of the plots had a peat depth of  $> 2$  m with the shallowest peats found in palm sites, which were at the edges of the peatland, and the deepest peats in the hardwood and stunted forest (Table 1). The physiochemical properties indicated that all sites, apart from one hardwood site, were characterised by fresh water conditions and that the peat was acid (Table 1): pH ranged between 3.5 and 4.5 and the conductivity ranged between ca. 100 and  $700 \mu\text{S cm}^{-1}$ . The peat in all plots was highly organic with high LOI ( $> 80\%$ ).

The palm sites had the greatest DON concentrations and subsequently the lowest C:N ratio in the porewater, while neither  $\text{NH}_4^+$  nor resin P differed among forest types. At palm sites the low C:N ratio in the peat solution together with a high  $E_{465}/E_{665}$  ratio suggest a large pool of less decomposed C in the dissolved fraction.

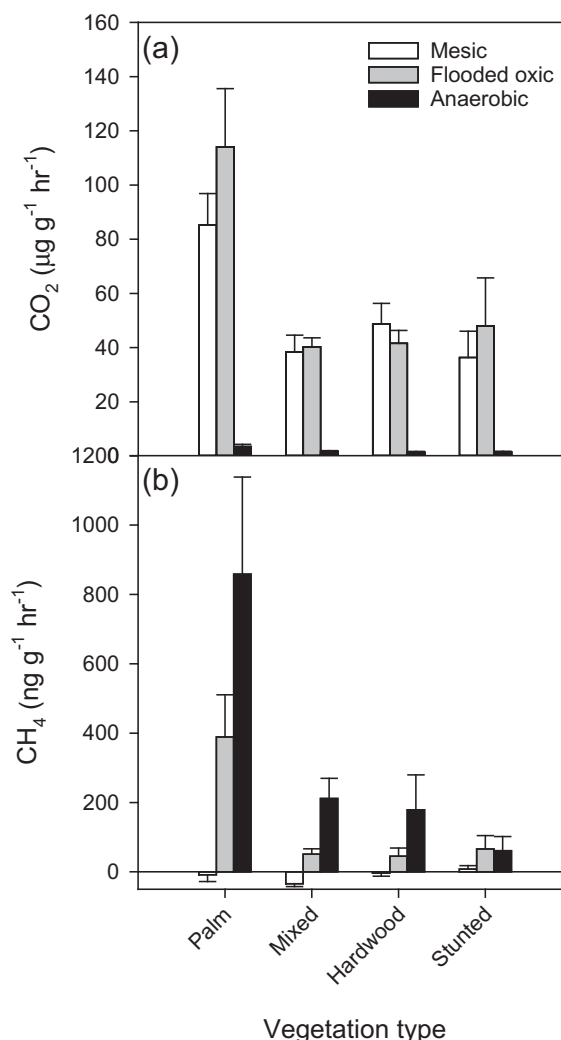
The in situ surface emissions of  $\text{CO}_2$  were lowest at the palm sites ( $< 400 \text{ mg m}^{-2} \text{ h}^{-1}$ ), with the highest ( $> 700 \text{ mg m}^{-2} \text{ h}^{-1}$ ) fluxes at the stunted forest sites. The in situ  $\text{CH}_4$  surface emissions ranged between  $1.3 \pm 0.5$  and  $32 \pm 23.7 \text{ mg m}^{-2} \text{ h}^{-1}$  (Table 1). During sampling, water level was close to the surface at all sites. Specifically, at palm sites ca. 90% of the surface was covered by water while the surface water coverage at mixed forest sites was ca. 50%.

**Table 1**

Peat properties measure in situ or from peat samples collected from the peat surface in different forest types during the field campaign. Mean and standard error of the mean are shown. \*\*\* $P < 0.001$ , \* $P < 0.05$ ,  $P < 0.1$ . Note that some of the measurements were only carried out at the major sites.

	Palm	Mixed	Hardwood	Stunted
All sites				
Peat depth (m)	$2.2 \pm 0.2$	$3.0 \pm 0.3$	$4.0 \pm 1.0$	$3.8 \pm 0.8$
pH	$4.34 \pm 0.14$	$4.28 \pm 0.27$	$4.24 \pm 0.75$	$3.65 \pm 0.05$
Conductivity ( $\mu\text{S}$ )	$135 \pm 17$	$110.3 \pm 18$	$718 \pm 604$	$94 \pm 10$
LOI (%)	$87.7 \pm 2.6$	$85.60 \pm 4.8$	$84.4 \pm 12.2$	$94.4 \pm 1.4$
DOC ( $\text{mg C g}^{-1}$ )	$10.7 \pm 2.9$	$5.8 \pm 2.4$	$6.3 \pm 5.6$	$1.7 \pm 0.5$
DON ( $\text{mg N g}^{-1}$ ) *	$7.2 \pm 2.0$	$2.2 \pm 1.2$	$2.3 \pm 2.1$	$0.2 \pm 0.1$
$\text{NH}_4^+$ ( $\mu\text{g N g}^{-1}$ )	$40.9 \pm 13.3$	$54.5 \pm 10.9$	$25.8 \pm 10.2$	$28.7 \pm 6.2$
$\text{PO}_4^{3-}$ ( $\mu\text{g P g}^{-1}$ )	$0.9 \pm 0.4$	$3.9 \pm 1.9$	$2.7 \pm 2.3$	$4.3 \pm 0.4$
$E_{465}/E_{665}$	$5.2 \pm 1.8$	$3.7 \pm 1.2$	$4.7 \pm 1.9$	$2.3 \pm 0.5$
C/N <sup>a</sup> ***	$1.9 \pm 0.4$	$3.6 \pm 0.4$	$3.6 \pm 0.8$	$7.0 \pm 0.4$
Major sites				
In situ $\text{CO}_2$ ( $\text{mg m}^{-2} \text{ h}^{-1}$ )	$369.4 \pm 57.9$	$575 \pm 85$	$527 \pm 20$	$753.0 \pm 186.3$
In situ $\text{CH}_4$ ( $\text{mg m}^{-2} \text{ h}^{-1}$ )	$1.3 \pm 0.5$	$1.3 \pm 1.2$	$20.0 \pm 17.1$	$32.0 \pm 23.7$
$T_{\text{soil}}$ ( $^{\circ}\text{C}$ )	$24.4 \pm 0.7$	$24.9 \pm 0.3$	$24.4 \pm 0.3$	$25.1 \pm 0.3$
$T_{\text{air}}$ ( $^{\circ}\text{C}$ )	$24.7 \pm 1.1$	$25.4 \pm 0.7$	$25.1 \pm 0.8$	$27.8 \pm 0.7$
Standing water (% area)	$90 \pm 5$	$50 \pm 13$	$70 \pm 17$	$70 \pm 7$
Depth of surface water pools (cm)	$12.4 \pm 1.9$	$13.3 \pm 3.9$	$18.2 \pm 6.3$	$8.1 \pm 0.6$

<sup>a</sup> Elemental ratio in the dissolved fraction.



**Fig. 2.** Fluxes of (a)  $\text{CO}_2$  and (b)  $\text{CH}_4$  from surface peat reflecting ex situ basal respiration from four forest types. The errors shown are standard error of the mean,  $n = 6$  for palm forest,  $n = 9$  for mixed forest,  $n = 3$  for hardwood forest and  $n = 3$  for student forest.

**Table 2**

Statistics describing treatment effects of forest type (Forest), moisture (M) and temperature (T) (fixed effects) on CO<sub>2</sub> and CH<sub>4</sub> fluxes from the laboratory incubations. CO<sub>2</sub> and CH<sub>4</sub> fluxes were log-transformed to meet the normality assumption. Significant effects are in bold.

Variate	Fixed effect	Wald statistic	n.d.f. <sup>a</sup>	F-value	d.d.f. <sup>b</sup>	P	SED
Log CO <sub>2</sub>	<b>Forest</b>	<b>16.25</b>	<b>3</b>	<b>5.41</b>	<b>16.2</b>	<b>&lt; 0.01</b>	<b>9.6</b>
	<b>M</b>	<b>1750.63</b>	<b>3</b>	<b>583.54</b>	<b>253.1</b>	<b>&lt; 0.001</b>	<b>6.1</b>
	<b>T</b>	<b>69.1</b>	<b>3</b>	<b>23.03</b>	<b>253.1</b>	<b>&lt; 0.001</b>	<b>6.1</b>
	Forest × M	10.21	9	1.13	253.1	0.3	13.8
	Forest × T	9.63	9	1.07	253.1	0.3	13.8
	<b>M × T</b>	<b>29.77</b>	<b>9</b>	<b>3.31</b>	<b>253.1</b>	<b>&lt; 0.001</b>	<b>12.2</b>
	Forest × M × T	18.16	27	0.67	253.1	0.9	25.0
Log CH <sub>4</sub>	Forest	9.48	3	3.13	15.8	0.055	135.6
	<b>M</b>	<b>121.36</b>	<b>3</b>	<b>40.45</b>	<b>254</b>	<b>&lt; 0.001</b>	<b>78.9</b>
	<b>T</b>	<b>52.82</b>	<b>3</b>	<b>17.61</b>	<b>254</b>	<b>&lt; 0.001</b>	<b>78.9</b>
	<b>Forest × M</b>	<b>33.48</b>	<b>9</b>	<b>3.72</b>	<b>254.1</b>	<b>&lt; 0.001</b>	<b>177.4</b>
	<b>Forest × T</b>	<b>26.81</b>	<b>9</b>	<b>2.98</b>	<b>254.1</b>	<b>&lt; 0.01</b>	<b>177.4</b>
	<b>M × T</b>	<b>51.86</b>	<b>9</b>	<b>5.76</b>	<b>254</b>	<b>&lt; 0.001</b>	<b>147.7</b>
	Forest × M × T	35.21	27	1.3	254.1	0.2	308.2

<sup>a</sup> Numerator degrees of freedom.

<sup>b</sup> Denominator degrees of freedom.

### 3.2. Gas fluxes from incubated samples

In contrast to the in situ flux measurement, maximum ex situ basal respiration of CO<sub>2</sub> and CH<sub>4</sub> from the surface peat samples were found at palm sites (Fig. 2 a and b, Table 2). For CH<sub>4</sub> emissions the mixed and hardwood forest had moderately high emissions, while the lowest emissions were from the stunted forest.

The moisture treatments strongly influenced CO<sub>2</sub> production, with comparable fluxes for the mesic and the oxic-flooded treatments, while fluxes were an order of magnitude lower in the anaerobic treatment (Fig. 2a, Table 2). For all forest types, CO<sub>2</sub> emissions increased exponentially with temperature in the flooded anaerobic and flooded oxic incubation, with CO<sub>2</sub> emissions being most temperature sensitive under the flooded oxic treatment with a Q<sub>10</sub> of 3.8 (Figs. 3a and 4a, Table 3). The temperature response was lowest for the mesic conditions during which the CO<sub>2</sub> emissions peaked at 25 °C and then dropped as temperatures increased. Note that peat moisture levels in the mesic treatment were slightly elevated in the 25 °C treatment compared to the other temperatures possibly (moisture content were 435 ± 38, 970 ± 100, 471 ± 42, 606 ± 74.7 in the 20, 25, 30 and 35 °C treatments, respectively). Variation in peat moisture levels within the mesic treatment was not significantly related to either CO<sub>2</sub> or CH<sub>4</sub> fluxes ( $P > 0.05$ ) and addition peat moisture as a covariate in the statistical models did not alter the temperature response of the CO<sub>2</sub> or CH<sub>4</sub> fluxes.

CH<sub>4</sub> emissions from peat were greatest under anaerobic conditions followed by the oxic flooded and mesic treatment (Fig. 2b, Table 2). Palm, mixed and hardwood forest had higher CH<sub>4</sub> emissions under anaerobic conditions, while peat from stunted forest sites was less responsive to the moisture treatments as indicated by the significant interaction between forest type and moisture treatment (Fig. 2b, Table 2). CH<sub>4</sub> was also emitted under flooded oxic conditions, but emissions dropped substantially under this treatment in the peat from the palm, mixed and hardwood forest sites. The net CH<sub>4</sub> uptake under mesic conditions was highest at the mixed forest sites.

Anaerobic CH<sub>4</sub> production increased exponentially with temperature (Q<sub>10</sub> > 6; Fig. 3b, Table 3), while temperature responses of CH<sub>4</sub> fluxes were weaker in the flooded oxic and mesic redox treatments, resulting in a significant Moisture × Temperature interaction (Table 2). This might be due to increased CH<sub>4</sub> consumption rates under oxic conditions as indicated by the negative CH<sub>4</sub> flux from the mesic samples, particularly at higher temperatures (Fig. 3b). The temperature response of CH<sub>4</sub> fluxes was most pronounced in peat from palm forests (Fig. 4b, Table 2).

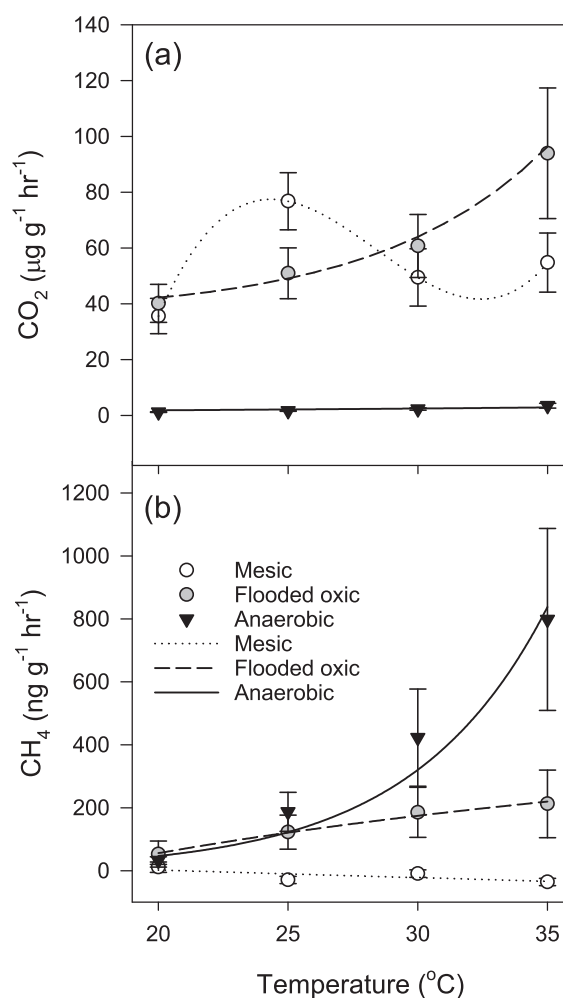


Fig. 3. Temperature response of (a) CO<sub>2</sub> fluxes and (b) CH<sub>4</sub> fluxes from the laboratory surface peat incubations, combining data from vegetation types. Means and standard error or the means are shown; lines are significant best fit regression models, of which exponential models were used for the Q<sub>10</sub> calculations in Table 3.

### 4. Discussion

The Q<sub>10</sub> values for CO<sub>2</sub> emissions were in the lower range of those previously reported for aerobic decomposition in peats from higher

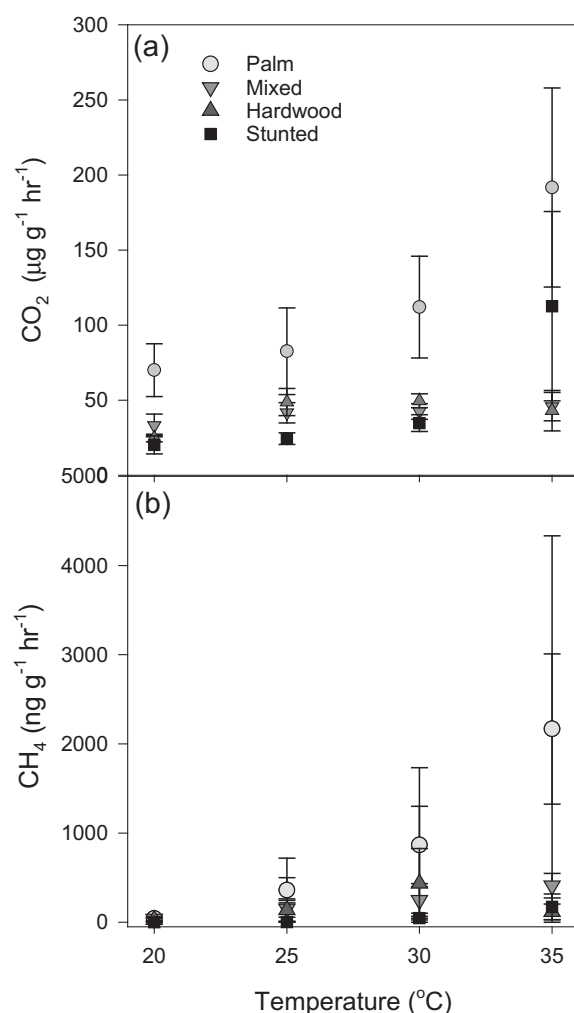


Fig. 4. Temperature response of (a) CO<sub>2</sub> fluxes from surface peat under flooded oxic conditions and (b) anaerobic CH<sub>4</sub> fluxes from laboratory incubations of peat from different forest types. Mean and standard error of the mean are shown.  $n = 6$  for palm forest,  $n = 9$  for mixed forest,  $n = 3$  for hardwood forest and  $n = 3$  for student forest.

Table 3

Q<sub>10</sub> (± SE) for the significant exponential models shown in Fig. 3. Q<sub>10</sub> is calculated using  $Q_{10} = e^{(10 \cdot k)}$ .

Moisture regime	CO <sub>2</sub>		CH <sub>4</sub>	
	Best fit model	Q <sub>10</sub>	Best fit model	Q <sub>10</sub>
Mesic	Cubic polynomial	n/a	Exponential growth <sup>a</sup>	2.7 ± 1.1
Flooded oxic	Exponential growth	1.8 ± 1.0	ns	n/a
Anaerobic	Exponential growth	1.3 ± 1.0	Exponential growth	6.8 ± 1.0

<sup>a</sup> Note that this relationship corresponds to CH<sub>4</sub> uptake, i.e. increasing negative fluxes with higher temperature (Fig. 3b).

latitude wetlands (range of Q<sub>10</sub> 1–16; Moore and Dalva, 1997; McKenzie et al., 1998; Inglett et al., 2012) and anaerobic CO<sub>2</sub> production found in subtropical peat (range 1.3–2.5; Inglett et al., 2012). As expected, the temperature response of CO<sub>2</sub> production was highest (Q<sub>10</sub> of 1.8) when neither O<sub>2</sub> nor water availability limited decomposition, showing that both anoxia and moisture deficiency limit the temperature response of CO<sub>2</sub> production. The low temperature response of CO<sub>2</sub> emissions from tropical peats is an important finding as it indicates that the temperature response of heterotrophic decomposition

in tropical wetland systems may be lower than in higher latitudes. This suggests that tropical systems may be less sensitive to rising temperatures with regards to CO<sub>2</sub> emission compared to colder wetlands. Similar low temperature responses of CO<sub>2</sub> production by microbial communities has been reported from well drained tropical lowland forest soils in Peru (Nottingham et al., 2015) and in Hawaii (Selmants et al., 2016). We speculate that the lower temperature response of the heterotrophic microbial community is linked to adaptations to the prevailing high temperatures in tropical environments. Indeed, lower temperature responses for tropical microbial communities have been linked to the generally high optimum temperatures (ca 25 °C of microbial biomass, CO<sub>2</sub> production and enzyme activities (Menichetti et al., 2015)).

The high CO<sub>2</sub> emissions in both oxic treatments (mesic and flooded oxygenated) (Fig. 2a) suggest that, in addition to water table drawdown (resulting in mesic surface condition), oxygen inputs with rainfall and from roots (Armstrong et al., 2006) may be strong drivers of aerobic decomposition processes below the water table. For example, the high in situ CO<sub>2</sub> emissions from tropical peatlands during periods of high rainfall (Wright et al., 2013) could be linked to inputs of oxygen via rainwater boosting heterotrophic respiration. With regards to the high CO<sub>2</sub> production from palm forest peat, relative to the other forest types, across all the moisture treatments, this may be due to greater amounts of higher quality – as indicated by the low C:N ratio in the peat solution (Table 1) – and quantity of substrates driven by the large total plant biomass at palm sites (Sjögersten et al., 2011). The strong difference in CO<sub>2</sub> emissions among vegetation types (i.e. higher at palm sites, Table 2 and Fig. 4) implicates the dominant vegetation as an important driver of microbial processes. Indeed, at our study site, specific microbial assemblages have been found to be associated with different dominate vegetation types (Troxler et al., 2012) indicating microbial adaptations to the prevailing litter inputs (Austin et al., 2014; Kaiser et al., 2014).

In contrast to the CO<sub>2</sub> emissions, anaerobic CH<sub>4</sub> production was highly temperature sensitive (Q<sub>10</sub> = 6.1) and in the upper range of Q<sub>10</sub> values reported for higher latitude peatlands (2 to 16; Dunfield et al., 1993; Turetsky et al., 2014). This clearly shows that the methanogenic microbial communities in tropical peatlands do not have lower temperature responses than those found in regions with colder climates. Furthermore, it indicates the potential for strong increases in CH<sub>4</sub> emissions from tropical wetlands in response to the higher temperatures associated with climate change. Given the current high CH<sub>4</sub> emissions from tropical wetlands (Melton et al., 2013) driven by large inputs of labile substrate from the vegetation (Sjögersten et al., 2014; Hoyos-Santillán et al., 2015 and 2016), such increases would have the potential to create strong positive feedbacks on the climate system. Furthermore, anaerobic CH<sub>4</sub> fluxes increased to a much greater extent than net CH<sub>4</sub> uptake from the mesic treatment (Q<sub>10</sub> = 2.7) as temperatures increased suggesting that increasing CH<sub>4</sub> production in response to higher temperatures would not be abated by increases in CH<sub>4</sub> uptake. Similar contrasting temperature responses of CH<sub>4</sub> production and consumption have been shown for a range of higher latitude peatlands (Turetsky et al., 2014). The net impact on CH<sub>4</sub> fluxes in the field will be modulated by the position of the water table and hence the zone in which CH<sub>4</sub> uptake occurs (Jauhiainen et al., 2005). Indeed, during periods of drought and low water tables the peatland system investigated here can act as a CH<sub>4</sub> sink (Wright et al., 2013). Therefore, if climate change results in lower water tables due to increased evapotranspiration and/or reduced precipitation (IPCC, 2013), conditions during which CH<sub>4</sub> uptake dominates may persist for longer time periods. Furthermore, the lower CH<sub>4</sub> production in the flooded oxic moisture treatment (Fig. 2b) indicates that high oxygen inputs (e.g. from rainfall or roots Hoyos-Santillán et al., 2016) can reduce CH<sub>4</sub> emissions by more than half, even when the peat remains completely waterlogged.

The controls posed by forest type on both anaerobic CH<sub>4</sub> production and its temperature response, i.e. greatest at palm sites (Fig. 4b,

Table 2), may be driven by greater labile substrate availability at palm sites (Wright et al., 2011). Our findings of contrasting temperature responses of CH<sub>4</sub> emissions among forest types in the tropics mirrors findings in higher latitude systems, where nutrient status and vegetation litter inputs have been shown to alter the temperature response of CH<sub>4</sub> emissions (Turetsky et al., 2014). Together, these findings implicate substrate quality (governed by vegetation litter inputs) as a critical control of the temperature response of CH<sub>4</sub> emissions across different latitudes. However, our data does not support the notion of more recalcitrant substrates driving greater temperature responses in tropical peatlands as postulated by the carbon quality hypothesis. Indeed, the Q<sub>10</sub> value of 1.8 that we found for CO<sub>2</sub> production under oxic flooded conditions (Table 3) is comparable for Q<sub>10</sub> values for aerobic heterotrophic CO<sub>2</sub> productions reported across a wide range of ecosystems (Davidson and Janssens, 2006). The differential temperature response of anaerobic CH<sub>4</sub> emissions among forest types indicates that climate warming impacts on emissions may differ substantially among areas covered by contrasting forest types, and also points towards the possibility of using vegetation type as a predictor for the responsiveness of CH<sub>4</sub> emissions of different wetland areas to climate warming.

When comparing the magnitude of the overall response of CO<sub>2</sub> and CH<sub>4</sub> fluxes to variation in soil moisture condition, temperature and forest type (significant or near significant main effects Table 2) the shift from anaerobic to mesic conditions created the greatest change in emissions (high CO<sub>2</sub> fluxes from mesic and flooded oxic treatments and high CH<sub>4</sub> fluxes from the two flooded treatments; Fig. 2) as expected. This compares to variation in field GHG emissions in response to fluctuating water tables in tropical peatlands in SE Asia (Jauhiainen et al., 2005; Couwenberg et al., 2010). Under high emission condition (Fig. 2 a and b) variation in forest type substantially modified emission rates (CO<sub>2</sub> fluxes from palm forest were 2–3 times higher than the other three forest types while CH<sub>4</sub> fluxes were ca. 4 times higher at palm forests). The CO<sub>2</sub> and CH<sub>4</sub> fluxes were 3 and 8 times higher, respectively, when comparing the 35 and 20 °C temperature treatment (flooded oxic and anaerobic treatments CO<sub>2</sub> and CH<sub>4</sub> fluxes, respectively). Together these findings suggest that GHG emissions from tropical peatlands are controlled by a range of strongly interacting factors.

In this study we investigated the temperature response of GHG production under controlled laboratory conditions to improve our understanding of the relative importance of different peat properties and moisture conditions for the temperature response of GHG fluxes from tropical peatlands as discussed above. However, the laboratory incubations we used in this study does not account for several important drivers of GHG emissions which may exert strong controls of GHG fluxes from tropical peatlands. For example, it is likely that labile C and oxygen input from roots into the peat matrix control variation in GHG emissions among different forest types (Joabsson et al., 1999; Ström et al., 2005; Hoyos-Santillán et al., 2016b). Furthermore, in our study we did not consider peat physical properties which are known to impact GHG fluxes as microaggregates may maintain peat CH<sub>4</sub> production also during periods of low water tables (Dunfield et al., 1993). In temperate soil systems processes of microbial acclimation/adaptation to elevated temperature have been shown to dampen temperature responses over time (Bradford et al., 2008; Kaiser et al., 2014). Such processes is important to consider in the context of our study as its short term nature does not allow us to evaluate what the long term in situ microbial responses to elevated peat temperatures, both with regards to activity levels and shifts in community composition, may be. Although, our findings cannot be used to quantify how in situ GHG fluxes will be affected by climate change, they suggest potential for strong temperature responses of GHG fluxes also in the tropics and the importance of exploring such temperature responses in the context of peat moisture conditions and forest type.

The greater temperature response of CH<sub>4</sub> fluxes than that of CO<sub>2</sub> fluxes suggests that climate warming may increase CH<sub>4</sub> emissions to a greater extent than CO<sub>2</sub> emissions under flooded conditions providing

substrate does not limit production. Based on the temperature relationships shown here (Fig. 3), assuming no microbial acclimation/adaptation to higher temperatures and that increased air temperatures would result in parallel increases in surface peat temperatures, a 3 °C warming by 2100, as predicted under the RCP8.5 scenario (IPCC, 2013), would generate a ca. 80% increase in CH<sub>4</sub> emissions from these ecosystems. However, if water tables drop, as discussed above, temperature-driven increases in emissions will be strongly modulated, and potentially mitigated against, by shifts in the moisture regime as methane oxidation processes as well as CO<sub>2</sub> production under mesic peat conditions also respond strongly to increasing temperatures.

## Acknowledgements

This work was funded by NERC (NE/J010820/1) to Sofie Sjögersten. Paul Aplin's fieldwork was supported through NERC grant NE/H003347/1. We thank Gabriel Jacome, Plinio Gondola, and Dayana Agudo from the Smithsonian Tropical Research Institute and James Verran at the University of Nottingham for their logistical support and laboratory assistance. We also thank Roberto Lopez for his assistance in the field.

## References

- Almeida, C.T., Oliveira-Júnior, J.F., Delgado, R.C., Cubob, P., Ramos, M.C., 2017. Spatiotemporal rainfall and temperature trends throughout the Brazilian Legal Amazon, 1973–2013. *Int. J. Climatol.* 37, 2013–2026.
- Armstrong, J., Jones, R.E., Armstrong, W., 2006. Rhizome phyllosphere oxygenation in Phragmites and other species in relation to redox potential, convective gas flow, submergence and aeration pathways. *New Phytol.* 172, 719–731. <http://dx.doi.org/10.1111/j.1469-8137.2006.01878.x>.
- Austin, A.T., Vivanco, L., González-Arzac, A., Pérez, L.I., 2014. There's no place like home? An exploration of the mechanisms behind plant litter-decomposer affinity in terrestrial ecosystems. *New Phytol.* <http://dx.doi.org/10.1111/nph.12959>.
- Bosatta, E., Ågren, G.I., 1999. Soil organic matter quality interpreted thermodynamically. *Soil Biol. Biochem.* 31, 1889–1891.
- Bradford, M.A., Davies, C.A., Frey, S.D., et al., 2008. Thermal adaptation of soil microbial respiration to elevated temperature. *Ecol. Lett.* 11, 1316–1327.
- Bridgman, S.D., Cadillo-Quiroz, H., Keller, J.K., Zhuang, Q., 2013. Methane emissions from wetlands: biogeochemical, microbial, and modelling perspectives from local to global scales. *Glob. Chang. Biol.* 19, 1325–1346. <http://dx.doi.org/10.1111/gcb.12131>.
- Chao, C., Chen, C.-A., Tu, J.-Y., 2008. Evaluating the “rich-get-richer” mechanism in tropical precipitation change under global warming. *J. Clim.* 22, 1982.
- Cheesman, A.W., Turner, B.L., Reddy, K.R., 2012. Soil phosphorus forms along a strong nutrient gradient in a tropical ombrotrophic wetland. *Soil Sci. Soc. Am. J.* <http://dx.doi.org/10.2136/sssaj2011.0365>.
- Cohen, A.D., Stack, E.M., 1996. Some observations regarding the potential effects of doming of tropical peat deposits on the composition of coal beds. *Int. J. Coal Geol.* 29, 39–65. [http://dx.doi.org/10.1016/0166-5162\(95\)00011-9](http://dx.doi.org/10.1016/0166-5162(95)00011-9).
- Couwenberg, J., Dommmain, R., Joosten, H., 2010. Greenhouse gas fluxes from tropical peatlands in south-east Asia. *Glob. Chang. Biol.* 16, 1715–1732. <http://dx.doi.org/10.1111/j.1365-2486.2009.02016.x>.
- Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440. <http://dx.doi.org/10.1038/nature04514>.
- Denmead, O., 2008. Approaches to measuring fluxes of methane and nitrous oxide between landscapes and the atmosphere. *Plant Soil* 309, 5–24. <http://dx.doi.org/10.1007/s11104-008-9599-z>.
- Dunfield, P., Knowles, R., Dumont, R., Moore, T.R., 1993. Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. *Soil Biol. Biochem.* 25, 321–326.
- Fierer, N., Craine, J.M., McLauchlan, K., Schimel, J.P., 2005. Litter quality and the temperature sensitivity of decomposition. *Ecology* 86, 320–326.
- Furukawa, Y., Inubushi, K., Ali, M., Itang, A.M., Haruo, T., 2005. Effect of changing groundwater levels caused by land-use changes on greenhouse gas fluxes from tropical peat lands. *Nutr. Cycl. Agroecosyst.* 71, 81–91.
- Grayson, R., Holden, J., 2012. Continuous measurement of spectrophotometric absorbance in peatland streamwater in northern England: implications for understanding fluvial carbon fluxes. *Hydrol. Process.* 26, 27–39. <http://dx.doi.org/10.1002/hyp.8106>.
- Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *J. Paleolimnol.* 25, 101–110.
- Hirano, T., Jauhiainen, J., Inoue, T., Takahashi, H., 2009. Controls on the carbon balance of tropical peatlands. *Ecosystems* 12, 873–887.
- Hooijer, A., Page, S., Canadell, J.G., et al., 2010. Current and future CO<sub>2</sub> emissions from drained peatlands in Southeast Asia. *Biogeosciences* 7, 1505–1514. <http://dx.doi.org/10.5194/bg-7-1505-2010>.



- org/10.5194/bg-7-1505-2010.
- Hoyos-Santillán, J., 2014. Controls of Carbon Turnover in Lowland Tropical Peatlands. The University of Nottingham <http://dx.doi.org/10.13140/2.1.3387.2329>.
- Hoyos-Santillán, J., Lomax, B.H., Large, D., et al., 2015. Getting to the root of the problem: litter decomposition and peat formation in lowland neotropical peatlands. *Biogeochemistry*. <http://dx.doi.org/10.1007/s10533-015-0147-7>.
- Hoyos-Santillán, H., Craigon, J., Lomax, B.H., Lopez, O.R., Turner, B.L., Sjögersten, S., 2016. Root oxygen loss from *Raphia taedigera* palms mediates greenhouse gas emissions in lowland Neotropical peatlands. *Plant Soil*. <http://dx.doi.org/10.1007/s11104-016-2824-2>.
- Inglett, K.S., Inglett, P.W., Reddy, K.R., Osborne, T.Z., 2012. Temperature sensitivity of greenhouse gas production in wetland soils of different vegetation. *Biogeochemistry* 108, 77–90.
- IPCC, 2013. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA (1535 pp.).
- Jauhainen, J., Takahashi, H., Heikkinen, J.E.P., Martikainen, P.J., Vasander, H., 2005. Carbon fluxes from a tropical peat swamp forest floor. *Glob. Chang. Biol.* 11, 1788–1797. <http://dx.doi.org/10.1111/j.1365-2486.2005.001031.x>.
- Joabsson, A., Christensen, T.R., Wallén, B., 1999. Vascular plant controls on methane emissions from northern peat forming wetlands. *Trends Ecol. Evol.* 14, 385–388.
- Kaiser, C., Franklin, O., Dieckmann, U., Richter, A., 2014. Microbial community dynamics alleviate stoichiometric constraints during litter decay. *Ecol. Lett.* 17, 680–690.
- Laiho, R., 2006. Decomposition in peatlands: reconciling seemingly contrasting results on the impacts of lowered water levels. *Soil Biol. Biochem.* 38, 2011–2024.
- Lelieveld, J., 1998. Changing concentration, lifetime and climate forcing of atmospheric methane. *Tellus Ser. B Chem. Phys. Meteorol.* 50, 128–150.
- Li, W., Dickinson, R.E., Fu, R., Niu, G.Y., Yang, Z.-L., Canadell, G.L., 2007. Future precipitation changes and their implications for tropical peatlands. *Geophys. Res. Lett.* 34, L01403. <http://dx.doi.org/10.1029/2006GL02836>.
- Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. *Funct. Ecol.* 8, 315–323.
- McKenzie, C., Schiff, S., Aravena, R., Kelly, C., St Louis, V., 1998. Effect of temperature on production of CH<sub>4</sub> and CO<sub>2</sub> from peat in a natural and flooded boreal forest wetland. *Clim. Chang.* 40, 247–266.
- Melton, J.R., Wania, R., Hodson, E.L., et al., 2013. Present state of global wetland extent and wetland methane modelling: conclusions from a model inter-comparison project (WETCHIMP). *Biogeosciences* 10, 753–788.
- Menichetti, L., Reyes Ortigoza, A.L., García, N., Giagnoni, L., Nannipieri, P., Renella, G., 2015. Thermal sensitivity of enzyme activity in tropical soils assessed by the Q10 and equilibrium model. *Biol. Fertil. Soils* 51, 299–310. <http://dx.doi.org/10.1007/s00374-014-0976-x>.
- Moore, T.R., Dalva, M., 1997. Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. *Soil Biol. Biochem.* 29, 1157–1164.
- Myers, R.G., Sharpley, A.N., Thien, S.J., Pierzynski, G.M., 2005. Ion-sink phosphorus extraction methods applied on 24 soils from the continental USA. *Soil Sci. Soc. Am. J.* 69, 511–521.
- Nahlik, A.M., Mitsch, W.J., 2011. Methane emissions from tropical freshwater wetlands located in different climatic zones of Costa Rica. *Glob. Chang. Biol.* 17, 1321–1334.
- Nottingham, A.T., Whitaker, J., Turner, B.L., Salinas, N., Zimmermann, M., Malhi, Y., Meir, P., 2015. Climate warming and soil carbon in tropical forests: insights from an elevation gradient in the Peruvian Andes. *Bioscience* 65 (9). <http://dx.doi.org/10.1093/biosci/biv109>.
- Oueslati, B., Bony, S., Risi, C., Dufresne, J.-L., 2016. Interpreting the inter-model spread in regional precipitation projections in the tropics: role of surface evaporation and cloud radiative effects. *Clim. Dyn.* 47, 2801–2815.
- Page, S.E., Rieley, J.O., Banks, C.J., 2011. Global and regional importance of the tropical peatland carbon pool. *Glob. Chang. Biol.* 17, 798–818. <http://dx.doi.org/10.1111/j.1365-2486.2010.02279.x>.
- Phillips, S., Rouse, G.E., Bustin, R.M., 1997. Vegetation zones and diagnostic pollen profiles of a coastal peat swamp, Bocas del Toro, Panama. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 128, 301–338.
- Roucoux, K.H., Lawson, I.T., Jones, T.D., et al., 2013. Vegetation development in an Amazonian peatland. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 374, 242–255.
- Selmants, P.C., Adair, K.L., Litton, C.M., Giardina, C.P., Schwartz, E., 2016. Increases in mean annual temperature do not alter soil bacterial community structure in tropical montane wet forests. *Ecosphere* 7 (4), e01296. <http://dx.doi.org/10.1002/ecs2.1296>.
- Sjögersten, S., Cheesman, A.W., Lopez, O., Turner, B.L., 2011. Biogeochemical processes along a nutrient gradient in a tropical ombrotrophic peatland. *Biogeochemistry* 104, 147–163. <http://dx.doi.org/10.1007/s10533-010-9493-7>.
- Sjögersten, S., Black, C.R., Evers, S., Hoyos-Santillán, J., Wright, E.L., Turner, B.L., 2014. Tropical wetlands: a missing link in the global carbon cycle? *Glob. Biogeochem. Cycles* 28, 1371–1386. <http://dx.doi.org/10.1002/2014GB004844>.
- Ström, L., Mastepanov, M., Christensen, T.R., 2005. Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. *Biogeochemistry* 75, 65–82.
- Treat, C.C., Wollheim, W.M., Varner, R.K., Grandy, A.S., Talbot, J., Frolking, S., 2014. Temperature and peat type control CO<sub>2</sub> and CH<sub>4</sub> production in Alaska permafrost peat. *Glob. Chang. Biol.* 20, 2674–2686.
- Troxler, T.G., 2007. Patterns of phosphorus, nitrogen and δ<sup>15</sup>N along a peat development gradient in a coastal mire, Panama. *J. Trop. Ecol.* 23, 683–691.
- Troxler, T.G., Ikenaga, M., Scinto, L., Boyer, J.N., Condit, R., Perez, R., Gann, G.D., Childers, D.L., 2012. Patterns of soil bacteria and canopy community structure related to tropical peatland development. *Wetlands* 32, 769–782. <http://dx.doi.org/10.1007/s13157-012-0310-z>.
- Turetsky, M., Kotowaska, A., Bubier, J., et al., 2014. A synthesis of methane emissions from 71 northern, temperate, and subtropical wetlands. *Glob. Chang. Biol.* 20, 2183–2197.
- Turner, B.L., Romero, T.E., 2010. Stability of hydrolytic enzyme activity and microbial phosphorus during storage of tropical rain forest soils. *Soil Biol. Biochem.* 42, 459–465.
- Uyguner, C.S., Bekbolet, M., 2005. Evaluation of humic acid photocatalytic degradation by UV–vis and fluorescence spectroscopy. *Catal. Today* 101, 267–274.
- van Hulzen, J.B., Segers, R., van Bodegom, P.M., Leffelaar, P.A., 1999. Temperature effects on soil methane production: an explanation for observed variability. *Soil Biol. Biochem.* 31, 1919–1929.
- VSN International, 2011. *GenStat for Windows*, 14th Edition. VSN International, Hemel Hempstead, UK Web page: [GenStat.co.uk](http://GenStat.co.uk).
- Wright, E., Black, C.R., Cheesman, A.W., Drage, T., Large, D., Turner, B.L., Sjögersten, S., 2011. Contribution of subsurface peat to CO<sub>2</sub> and CH<sub>4</sub> fluxes in a neotropical peatland. *Glob. Chang. Biol.* 17, 2867–2881. <http://dx.doi.org/10.1111/j.1365-2486.2011.02448.x>.
- Wright, E.L., Black, C.R., Turner, B.L., Sjögersten, S., 2013. Environmental controls of temporal and spatial variability in CO<sub>2</sub> and CH<sub>4</sub> fluxes in a neotropical peatland. *Glob. Chang. Biol.* 19, 3775–3789. <http://dx.doi.org/10.1111/gcb.12330>.